



What happens after mussels die? Biogenic legacy effects on community structure and ecosystem processes[☆]

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ABSTRACT

Mussels are well-known ecosystem engineers in soft-bottom systems. *Mytilus edulis* beds have myriad effects on sediment, benthic organisms, and ecosystem processes such as hydrodynamic transport of sediment and animals. When mussels die, they may leave behind massive amounts of whole (empty) and fragmented shells. The legacy effects of this long-lasting biogenic material (i.e., shell hash) on benthic systems are poorly understood. We measured percent cover values of 4 bottom cover types, i.e., live mussels, whole shells, fragmented shells, and bare sediment, at the mussel bed in Carrying Place Cove, Harrington, Maine, USA, and examined their effects on sediment characteristics, community structure of macrofauna and meiofauna, and ecosystem processes of sediment flux and dispersal of postlarval macrofauna and meiofauna. We predicted that live mussels are the cover type with the greatest effects compared to bare sediment, followed by fragmented shells and then whole shells. We discovered mostly bare sediment, substantial cover of whole and fragmented shells, and almost no live mussels in what had in past years been a robust bed. We found significant univariate and multivariate differences in sediment and animals across cover types, especially for meiofauna. Fragmented shell material in particular may be an important driver in this system. Our results are the first to quantify the 4 mussel bed cover types and demonstrate their effects. Mussel beds in the Gulf of Maine have experienced severe declines in the past two decades, attributed primarily to climate change and the invasive green crab, *Carcinus maenas*. Our results may be useful in predicting the responses of soft-bottom systems as intact mussel beds die off, leaving large areas of bare sediment and shell hash.

1. Introduction

Mussels are well-known ecosystem engineers in soft-bottom systems. Blue mussel (*Mytilus edulis*) beds have myriad effects on sediment, infauna, epifauna, and ecosystem processes like wind-generated bed-load transport and animal dispersal (Bouma et al., 2009; Buschbaum et al., 2009; Commito et al., 2005, 2008; Gutiérrez et al., 2011). When soft-bodied ecosystem engineers such as polychaetes die, their impact may soon begin to wane (Gutiérrez et al., 2011; Reise, 2002). But mussels and other hard-bodied ecosystem engineers may leave behind massive amounts of whole (empty) and fragmented shells (Fig. 1A; Commito et al., 2008, 2014). The legacy effects of this long-lasting biogenic material (i.e., shell hash) on community structure and ecosystem processes are poorly understood.

Mussel beds consist of intermingled patches of live mussels, bare sediment, and whole and fragmented shells (Fig. 1B). Because beds in Maine have a hierarchical, fractal spatial structure down to the millimeter scale (Snover and Commito, 1998; Commito and Rusignuolo, 2000; Commito et al., 2016), even a small mussel bed patch may consist of smaller patches of all 4 components. Moreover, live mussels attach to each other and to whole and fragmented shells, bound together by byssal threads. Thus, ecosystem engineering effects of mussel beds cannot be attributed solely to the live mussel component. Yet to our knowledge, no study of the effects of mussel shell hash has ever been conducted at an intertidal, soft-bottom mussel bed anywhere in the world.

Mollusk shell material can have important impacts on habitat provision, water flow, recruitment, food supply, predation, and other

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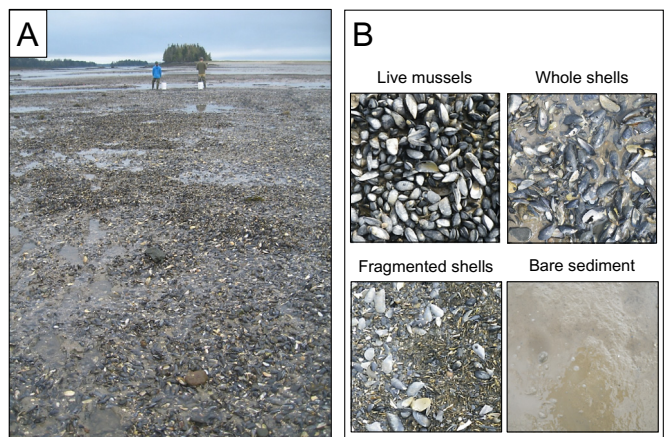


Fig. 1. Mussel bed bottom cover. (A) Shell hash at our mussel bed study site: Carrying Place Cove, Harrington, Maine, USA. (B) Types of bottom cover found in Maine mussel beds.

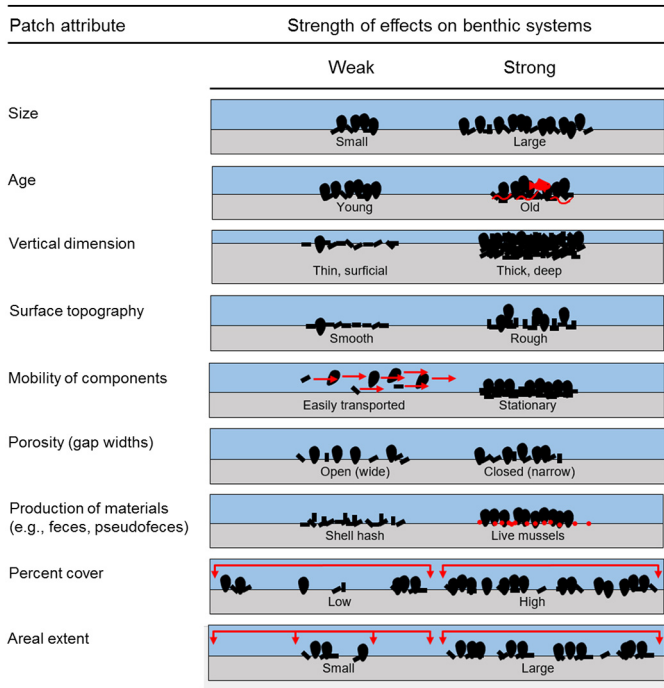


Fig. 2. Mussel bed patch characteristics. Attributes presented across the range from weak to strong effects on soft-bottom sediment, community structure, and ecosystem processes of sediment flux and animal transport in bedload.

factors (Gutiérrez et al., 2003, 2011), often causing an increase in in-fauna, epifauna, and species diversity in benthic systems (Guay and Himmelman, 2004; Gutiérrez et al., 2003; Hily, 1991; Hubbard, 2016; Kraeuter et al., 2003; Ribeiro et al., 2005; Rodney and Paynter, 2006; Summerhayes et al., 2009; Tomatsuri and Kon, 2017; Wilding and Nickell, 2013). However, some studies have found mixed, weak, or no significant effects (Bomkamp et al., 2004; Gutiérrez and Iribarne, 1999; Hewitt et al., 2005; Mann et al., 2016; Nicastro et al., 2009; Turner et al., 1997). The wide-ranging responses to living bivalves and non-living biogenic structure make it difficult to predict the expected magnitude and even the direction of differences among live mussels, whole shells, and fragmented shells relative to bare sediment. The impacts most likely stem from variations in bed patch attributes such as those presented in Fig. 2.

It seems plausible that effects on ambient sediment and organisms, as well as on flow-related sediment flux and animal transport, are

greatest for live mussels, followed by fragmented shells and then whole shells. We make this prediction because live mussels produce copious amounts of feces and pseudofeces that increase the silt-clay fraction and create low-oxygen, high sulfide conditions that are detrimental to most species but favorable to a few others, e.g., the oligochaete *Tubificoides benedeni* and opportunistic polychaetes like *Capitella capitata* (Albrecht and Reise, 1994; Albrecht, 1998; Commito et al., 2005, 2008; Kent et al., 2017; Ragnarsson and Raffaelli, 1999). In addition, live mussels project up into the water column above the bottom, and this roughness profile has strong effects on flow dynamics that increase the capture of sediment, postlarval macrofauna, and meiofauna moving across the bottom (Commito and Rusignuolo, 2000; Commito et al., 2005).

Fragmented shells may be next in importance because they can often be observed in dense, tightly packed patches that may act as a barrier between the sediment and the water column. Packing theory demonstrates clearly that packing is tighter, with lower porosity, when the objects are of many sizes, allowing small ones to fill in the gaps between large ones (Chen et al., 2003). Thus, at our sites in Maine we observe that fragmented shell pieces, which exist in angular shapes of all sizes, are generally more tightly packed than whole shells. Fragmented shells also alter sediment structure by contributing directly to the coarse sediment fraction. Species abundances in Maine mussel beds can be positively or negatively correlated with coarse, terrestrially-derived gravel (Commito et al., 2008), so they may respond similarly to coarse, fragmented shell material as well. In particular, fragmented shells might be expected to depress animal abundance by blocking the movement of oxygen into the sediment below. Their influence on flow dynamics, hence the movement of sediment and animals, is probably less than that of live mussels because fragments do not project as high up into the water column.

Whole shells are often loosely packed. They are generally larger than fragments, and their large-radius curves leave sizable gaps between neighboring shells even when touching because they have no straight, parallel sides. This porosity due to gaps within a patch may create less of a sediment-water column barrier compared to fragmented shell cover. We also observe that whole shells tend to lie flat on the bottom, often concave-side down, presenting a relatively smooth bed surface that may not induce as much turbulent flow as does a bed with the rough topography of live mussels or fragmented shell pieces. Thus we expect whole shells to have less of an impact on sediment, animals, and hydrodynamics than do live mussels and fragmented shells.

In this study we investigated biogenic legacy effects by comparing sediment characteristics, community structure of macrofauna and meiofauna, and the ecosystem processes of sediment flux and faunal transport in isolated patches of live mussels, bare sediment, whole shells, and fragmented shells in a Maine soft-bottom mussel bed. Mussel beds in the Gulf of Maine have recently experienced severe declines, with reduced larval settlement and decimated abundances of juveniles and adults in the past two decades (Petraitis and Dudgeon, 2015; Sorte et al., 2011, 2016). The bottom cover proportions of whole shells, fragmented shells, and bare sediment may be increasing relative to that of live mussels. If so, our results could be useful in understanding how soft-bottom systems respond to the apparent mussel bed decline.

2. Methods

2.1. Study site

The research was conducted at the intertidal, soft-bottom *Mytilus edulis* bed in Carrying Place Cove, Harrington, Maine, USA (44.5451°N, –67.7844°W), a relatively protected embayment with a bottom of muddy sand (Fig. 3). As is typical in this region, the bed extends across the mouth of the cove near the low tide line. The ecology of eastern Maine soft-bottom mussel beds like this one has been well studied, including their spatial abundance patterns (Commito et al., 2006, 2014; Crawford et al., 2006), sediment and macrofauna (Commito et al.,

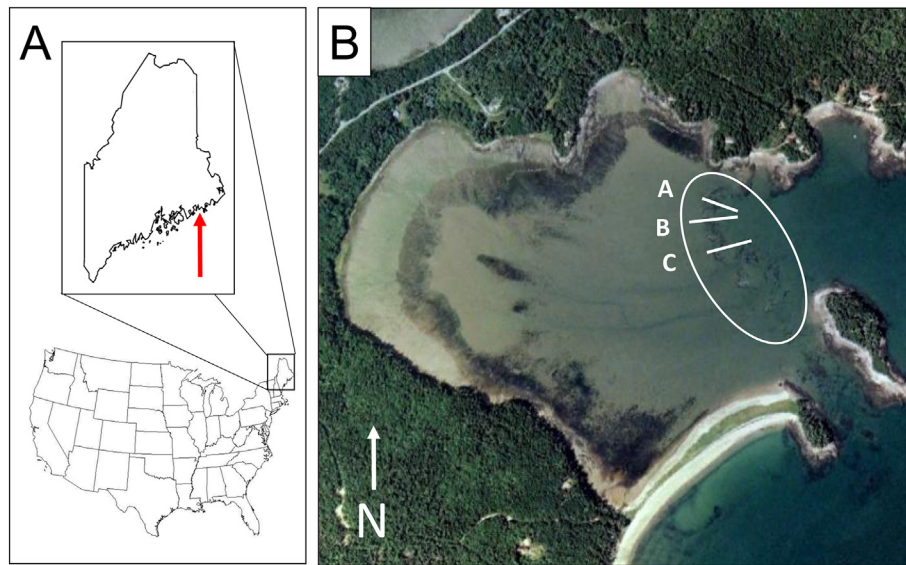


Fig. 3. (A) Location of study site in eastern Maine, USA. (B) Aerial view of Carrying Place Cove, Harrington, Maine, with mussel bed and transects indicated. Cores were taken and traps deployed immediately south of Transect C. Map data copyright 2015 Google.

2005, 2008), and impacts on sediment flux and postlarval dispersal dynamics (Commito et al., 2005). The intertidal, soft-bottom mussel beds in eastern Maine that we have studied for decades typically had $\approx 50\%$ cover of live mussels in complex fractal power-law spatial patterns (Commito et al., 2006, 2014; Crawford et al., 2006). The remaining bed surface consisted primarily of bare sediment with small percent cover values of whole (empty) mussel valves and mussel shell fragments. Today, some of the largest, densest beds where we have conducted research since the mid-1970s contain virtually no live mussels (John A. Commito, personal observation; Brian F. Beal, personal communication). Our original intent was to conduct this investigation at the nearby Guard Point mussel bed because we had results from past studies there for possible comparison (Commito et al., 2005, 2006, 2014). However, we could not locate any live mussels except for some scattered individual on this once thriving bed, requiring us to move ≈ 1 km to Carrying Place Cove, which has similar sediment and other characteristics. No long-term time series of aerial photographs suitable for mussel cover analysis exists for Carrying Place Cove. However, our field observations at the site over the last 30 years suggest that mussel abundance at Carrying Place Cove has dropped precipitously, resulting in a scattered array of small, isolated patches of live mussels in a complex pattern with bare sediment, whole mussel shells, and mussel shell fragments over the bed surface (Fig. 1A).

In this project we used photo transects to quantify the percent cover of each of the 4 cover types: live mussels, whole mussel shells, fragmented mussel shells, and bare sediment. In patches of each cover type, we used: (1) core samples to compare univariate and multivariate measures of sediment characteristics, macrofauna, and meiofauna; and (2) bottom traps to compare the ecosystem processes of sediment flux and dispersal of postlarval macrofauna and meiofauna.

2.2. Cover types

Digital photographs were taken every meter along 3 transects (Transect C on 4 August 2011, Transects A and B on 31 July 2012) that ran from the upper to the lower margin of the mussel bed (Fig. 3). No transects were established in the southern portion of the bed because of possible effects on the bottom in that area from occasional light activity by small boats. Images were cropped to an area of 0.25 m^2 . They were uploaded into ArcMap and hand digitized into the 4 cover types (live mussels, whole shells, fragmented shells, and bare sediment). Percent cover of each cover type was determined using pixel counts. Transect

results were plotted with a 3-cell running average for smoothing.

2.3. Ambient sediment, macrofauna, and meiofauna

We followed Hurlburt's (1984) recommendations for treatment interspersal when spatial heterogeneity is expected, particularly in field projects of this size. Our sample design utilized his systematic model to achieve treatment interspersal, reducing the likelihood of treatment segregation, type 1 error, and spurious treatment effects. Our goal had been to sample large patches similar in size to those from a previous study at Guard Point, where we were able to select live mussel patches $\geq 6.0 \text{ m}$ in the smallest dimension (Commito et al., 2005). Although we commonly observed such large patches in past years at Carrying Place Cove, none approaching that size could be found at the time of this study. Live mussel patches were smaller and far less common than the other 3 cover types, so we searched for live mussels and chose the 10 mussel patches $\geq 0.5 \text{ m} \times 0.5 \text{ m}$ in size nearest to Transect C within a $\approx 10 \text{ m}$ wide band from the upper to the lower mussel bed margin ($\approx 100 \text{ m}$). We then selected the patches $\geq 0.5 \text{ m} \times 0.5 \text{ m}$ of each of the other 3 cover types closest to each live mussel patch. Thus, $N = 10$ for each of the 4 cover types.

At low tide on 15 May 2011, 1.3 cm diameter cores (cross-sectional area = 1.33 cm^2) were taken to a depth of 5 cm at the 40 sampling locations. Cores of this size were used successfully to sample sediment characteristics, macrofauna, and meiofauna at similar sites nearby, collecting approximately the same numbers of macrofaunal species as larger cores and allowing us to utilize a larger sample size with the same sampling and laboratory processing effort (Commito and Tita, 2002; Commito et al., 2005, 2008). Core contents were stained with rose bengal and fixed in situ with buffered formalin. In the laboratory, samples were wet sieved on 0.5 mm (to obtain macrofauna and the coarse sediment fraction) and 0.063 mm (meiofauna and fine sediment fraction) mesh, and the material that passed through the sieves (silt-clay sediment fraction) was retained. Macrofauna (to species level when possible, using Pollock, 1998) and meiofauna (to family or higher levels, e.g., Copepoda, Nematoda, Foraminifera) were identified and counted in gridded Petri dishes. The 3 sediment size-classes were dried at 85°C for 24 h and weighed. Organic matter was calculated using loss-on-ignition by burning at 500°C for 4 h (Dean, 1974).

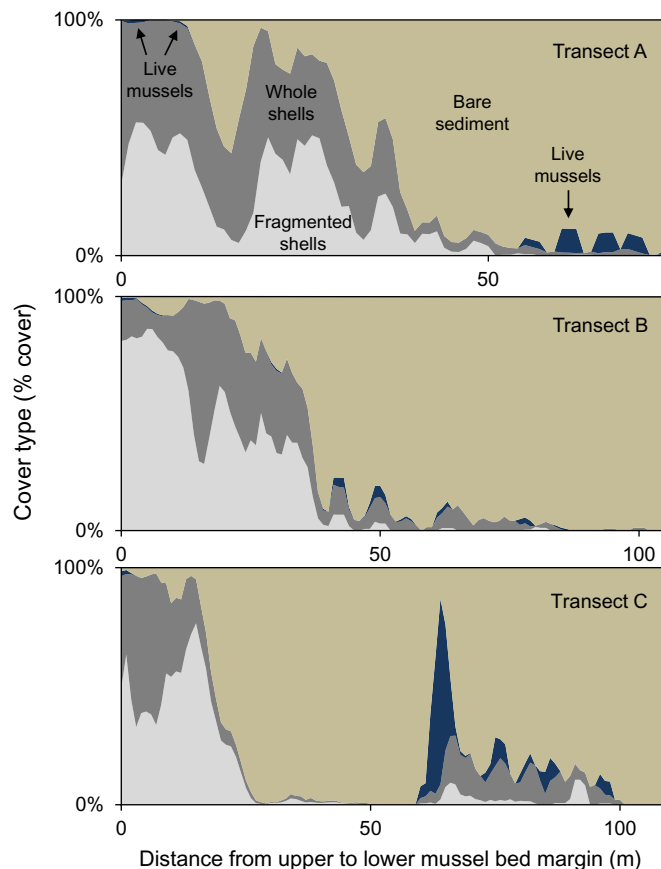


Fig. 4. Percent cover values for cover types along transects. Note different transect lengths on horizontal axes. See Table 1 for summary values.

2.4. Sediment flux and animal dispersal as ecosystem processes

On 15 May 2011, 15.0 cm tall bottom traps of the same diameter as the coring device (aspect ratio = 11.5:1) were filled with seawater and inserted flush with the sediment surface into the holes created during the core sampling described above. Traps of this design were used successfully to measure sediment flux and dispersal of macrofauna and meiofauna at similar sites nearby (Commito and Tita, 2002; Commito et al., 2005). To assure that the traps did not lose their capture efficiency by filling with sediment and effectively lowering their aspect ratio, they were removed and replaced with new traps inserted into the same holes at low tide on each of the following 3 days. Trap samples were processed in the same way as the cores. Data from the daily trap contents were combined to create a cumulative sample for the 3 day deployment period. Following Commito et al. (1995a, 2005) and Commito and Tita (2002), the sediment flux rate = g sediment trap⁻¹ deployment⁻¹ and the animal dispersal rate = number of individuals trap⁻¹ deployment⁻¹ were calculated. Despite being marked with flags, some traps were impossible to locate due to burial by shell hash moved by water currents. Because our multivariate statistical approach (see below) required a balanced design, trap samples from each cover type were eliminated at random to achieve an equal number of replicates ($N = 8$) for each cover type.

2.5. Data analysis

Analysis of the cores and traps included the sediment mass in each size-class (silt-clay, fine sand, coarse material) and percent organic matter, as well as the total abundance, species richness, Shannon-Wiener Index (H') using log base e , and abundance of each dominant taxon in the macrofauna and meiofauna, respectively. Because the

oligochaete *Tubificoides benedini* often dominates the macrofauna in mussel beds and exhibits abundance patterns different from other macrofaunal species (Commito et al., 2005, 2008), the non-oligochaetes were also analyzed together as one group.

For each core and trap variable, differences among cover types (4 levels: fixed) were analyzed with a 1-factor ANOVA. Homogeneity of variances was checked using Cochran's C-test, and, when necessary, data were transformed to reduce heterogeneity to acceptable levels, as indicated in the ANOVA tables. In these cases, back-transformed means and 95% confidence intervals were calculated. When significant differences among cover types were found ($\alpha = 0.05$), a posteriori comparisons were made using SNK tests. Cases occurred where SNK could not discriminate among alternative hypotheses despite the significant ANOVA differences. Because a posteriori multiple comparisons have less power than the original ANOVA F -test, such cases indicated that the 2 cover types with the largest and smallest means were significantly different, and no further resolution among cover types could be determined (Underwood, 1997). All analyses were done with the GMAV 5 computer program (A. J. Underwood and M. G. Chapman, unpublished).

For macrofauna and meiofauna in the ambient community and dispersing assemblages, differences among cover types (4 levels: fixed) were analyzed with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity measures (Anderson, 2001; McArdle and Anderson, 2001). Raw, square root transformed, and presence/absence data were used in the analysis. Results were the same for all 3, so only results from raw data are presented. PERMDISP was utilized to determine if significant PERMANOVA differences were due to cover type data dispersion or location in multivariate space (Anderson, 2006; Anderson et al., 2006). PERMANOVA and PERMDISP were executed using the functions “adonis” and “betadisper” in the “vegan” package for R v3.4.2 (R Core Development Team, 2015). The non-metric multidimensional scaling (nMDS) ordination model based on the Bray-Curtis dissimilarity matrix was conducted with the PRIMER v5.2 package (Clarke and Warwick, 2001) to visualize cover type separation when PERMANOVA differences were significant.

3. Results

3.1. Cover types

The 3 transects revealed consistent trends from the upper margin to the lower margin of the mussel bed (Fig. 4, Table 1). Live mussel cover was only 1–4% of the bed surface. A few individuals were found at the upper margin of the bed, but most were in the lower part of the bed near the low tide line. Whole shell cover (7–21%) and fragmented shell cover (4–15%) were much more extensive, particularly in the upper portion of the bed. Bare sediment (62–88%) was by far the largest cover type, especially in the middle and low portions of the bed.

Table 1

Cover values for 3 transects at Carrying Place Cove. Values may not add up to 100% due to rounding. Transects extended from the upper margin to the lower margin of the mussel bed. See Fig. 3 for aerial view of the cove and Fig. 4 for transect details.

Transect	Length (m)	Cover (%)			
		Live mussels	Whole shells	Fragmented shells	Bare sediment
A	76	1.5	21.3	15.2	61.8
B	107	0.7	6.6	4.0	88.7
C	112	3.7	10.1	10.4	75.3

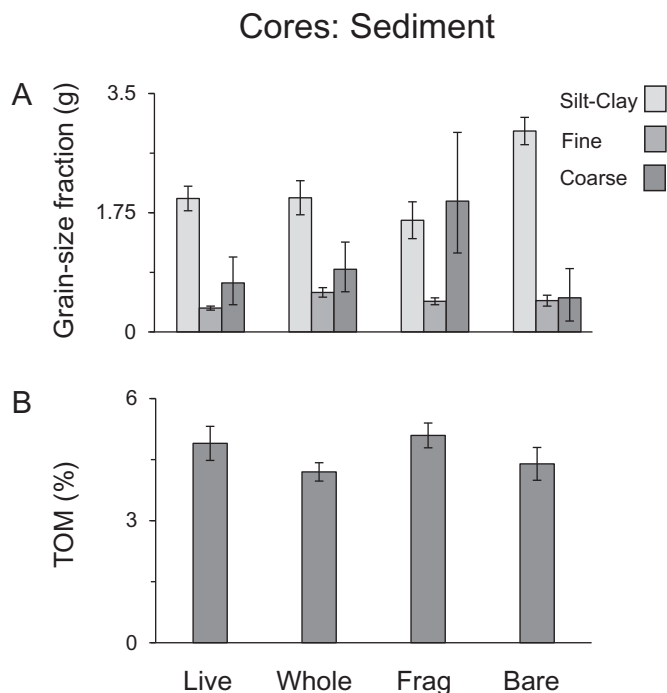


Fig. 5. Sediment results for cores. (A) Mass values of silt-clay (light gray), fine sand (medium gray), and coarse material (dark gray). (B) Percent total organic matter (TOM). Values are mean \pm 1 SE, except back-transformed mean and 95% confidence interval for coarse material, which required transformation to meet ANOVA assumptions. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. See Results and Table 2 for statistical analysis.

3.2. Ambient sediment, macrofauna, and meiofauna

The silt-clay and coarse sediment size-classes were significantly different among cover types (Fig. 5, Table 2). Silt-clay mass was

Table 2
ANOVA results for ambient community cores.

Parameter	Transform	$F_{3,36}$	P	SNK
Sediment				
Silt-clay (g)		4.78	0.005	Bare > Whole = Live = Frag
Fine sand (g)		2.1	0.117	
Coarse material (g)	Ln(X + 1)	5.51	0.002	Frag > Whole = Live = Bare
Total organic matter (%)		1.47	0.24	
Macrofauna				
Number of species		2.09	0.119	
H'		0.92	0.439	
Total abundance	Ln(X + 1)	1.22	0.318	
Oligochaetes		1.89	0.149	
Non-oligochaetes	Ln(X + 1)	1.73	0.179	
<i>Capitella capitata</i>	Ln(X + 1)	3.34	0.03	NAH (Live > Frag)
Meiofauna				
Number of taxa		0.51	0.678	
H'		1.53	0.223	
Total abundance		4.21	0.012	NAH (Bare > Whole)
Nematodes		4.4	0.01	NAH (Bare > Whole)
Copepods		2.66	0.065	
Foraminiferans		2.35	0.089	

Significant differences ($P < 0.05$) are in **bold**. For parameters with significant differences among cover types, the SNK results are presented. NAH = no alternative hypothesis; the 2 cover types with the largest and smallest means were significantly different, and no further resolution among cover types was possible. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment.

significantly greater in cores from the bare sediment cover type than from the other cover types, which were not significantly different from each other. Coarse material mass was significantly greater in cores from the fragmented shell cover type than from other cover types, which were not significantly different from each other (Table 2). The percentage of organic material did not vary significantly among cover types (Fig. 5, Table 2).

Sixteen macrofaunal species were found (Appendix A), of which the most abundant was the oligochaete *Tubificoides benedini* (74% of the total), followed by the polychaete *Capitella capitata* and much smaller numbers of the other species. No significant differences were found among cover types except for *C. capitata* abundance (Fig. 6, Table 2). The a posteriori comparison test could not discriminate among alternative hypotheses, indicating that *C. capitata* was significantly more abundant in live mussel cover than in fragmented shell cover, and no further resolution among cover types was possible (Table 2). At the multivariate level, PERMANOVA revealed no significant differences in macrofaunal community structure among cover types with or without oligochaetes (Table 3).

Six meiofaunal taxa were found (Appendix A), of which the most abundant were nematodes (81% of the total), followed by copepods, foraminiferans, and much smaller numbers of the other taxa. Total abundance and nematode abundance were significantly different among cover types (Fig. 7, Table 2). In both cases the a posteriori comparison test could not discriminate among alternative hypotheses, indicating that total meiofauna and nematodes were significantly more abundant in bare sediment cover than in whole shell cover, and no further resolution among cover types was possible (Table 2). At the multivariate level, PERMANOVA revealed significant differences in meiofaunal community structure among cover types (Table 3), and nMDS plots showed separation among cover types (Fig. 8), consistent with the PERMDISP result of no significant data dispersion ($F_{3,36} = 0.47$, $P = 0.74$). Dissimilarity values were large for fragmented and whole shells compared to bare sediment and, to a lesser degree, live mussels, highlighting the impact of shell hash on meiofaunal community structure.

3.3. Sediment flux and animal dispersal as ecosystem processes

The silt-clay and coarse sediment size-classes collected by traps were significantly different among cover types (Fig. 9, Table 4). In both cases the a posteriori comparison test could not discriminate among alternative hypotheses, indicating that trap values were significantly higher for silt-clay in live mussel cover than fragmented shell cover and for coarse sediment in fragmented shell cover than live mussel cover, and no further resolution among cover types was possible (Table 4). Total sediment mass collected by traps was not significantly different among cover types (Table 4), nor was the percentage of organic material (Fig. 9, Table 4).

Twenty-four macrofaunal species were found in traps, and the species ranks were different from those in the ambient community cores (Appendix A). The most abundant species was still *Tubificoides benedini*, but dropping to 43% of the total, followed by smaller numbers of other species, with no species a clear co-dominant, including *Capitella capitata*. No significant differences were found for any macrofaunal species, total abundance, species richness, or H' (Fig. 10, Table 4). At the multivariate level, PERMANOVA revealed no significant differences in macrofaunal dispersal assemblage structure among cover types (Table 5).

Eight meiofaunal taxa were found in traps, and the taxon ranks were different from those in cores, with a dramatic shift to copepods as the dominant taxon (54% of the total), followed by nematodes, foraminiferans, and much smaller numbers of the other taxa (Appendix A). Total abundance was significantly lower in traps from fragmented shell cover than from other the cover types, which were not significantly different from each other (Fig. 11, Table 4). H' and the abundances of

Cores: Macrofauna

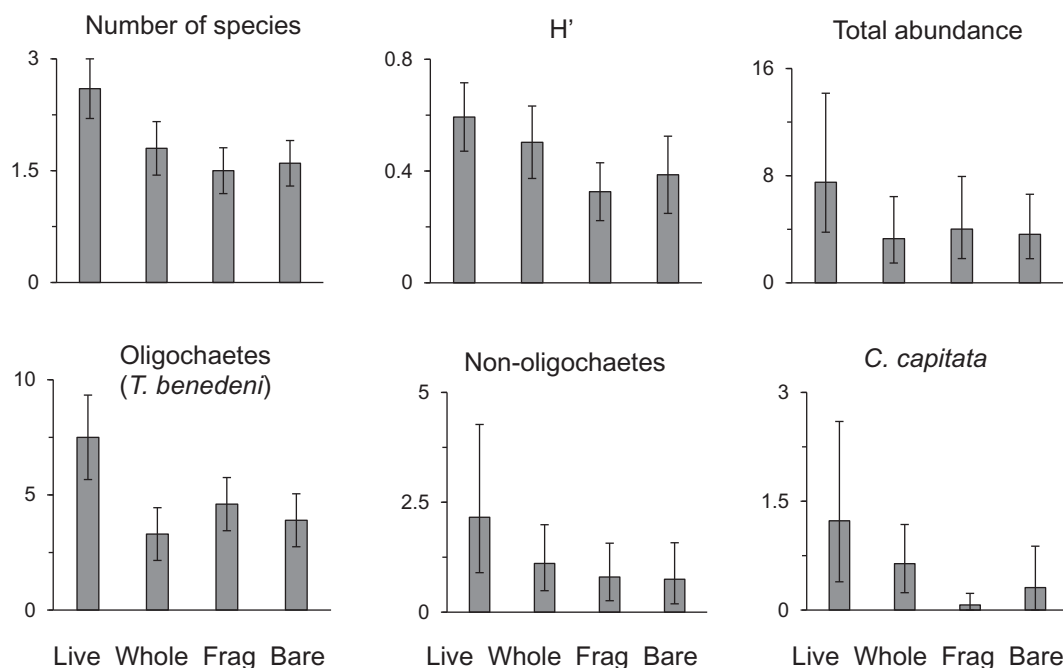


Fig. 6. Macrofauna results for cores. Values are mean \pm 1 SE for number of species, Shannon-Wiener diversity index (H'), and abundance of the dominant species (the oligochaete *Tubificoides benedeni*), and back-transformed mean and 95% confidence interval for total abundance, the non-oligochaetes as a group, and the second most abundant species (the polychaete *Capitella capitata*), which required transformation to meet ANOVA assumptions. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. See Results and Table 2 for statistical analysis.

Table 3
PERMANOVA results for ambient community cores.

Parameter	MS	$F_{3,36}$	P
Macrofauna			
All species	3118.75	0.24	0.275
Without oligochaetes	5283.76	1.44	0.275
Meiofauna	3364.62	2.48	0.031
Within cover type:			
Live = 43.53			
Whole = 49.23			
Frag = 49.61			
Bare = 39.91			
Among cover types:			
Live vs Whole = 48.88			
Live vs Frag = 48.24			
Live vs Bare = 42.67			
Whole vs Frag = 47.69			
Whole vs Bare = 54.22			
Frag vs Bare = 55.53			

Significant differences ($P < 0.05$) are in **bold**. For parameters with significant differences among cover types, the mean Bray-Curtis dissimilarity (%) values within and among cover types are presented. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment.

nematodes and foraminiferans also differed significantly among cover types (Fig. 11, Table 4). In all 3 cases the a posteriori comparison test could not discriminate among alternative hypotheses, indicating that trap values were significantly higher for H' in bare sediment than live mussels, nematodes in bare sediment than fragmented shells, and foraminiferans in bare sediment than live mussels, and no further resolution among cover types was possible (Table 4). At the multivariate level, PERMANOVA revealed significant differences in meiofaunal community structure among cover types (Table 5), and the nMDS plot showed separation among cover types (Fig. 8), consistent with the

PERMDISP result of no significant data dispersion ($F_{3,28} = 0.97$, $P = 0.45$). Dissimilarity values were large for fragmented shell cover compared to all the other cover types (Table 5), demonstrating its important impact on the meiofaunal dispersal assemblage.

4. Discussion

4.1. Mussel bed cover

The results presented here are the first to quantify live mussel, whole shell, fragmented shell, and bare sediment percent cover values and demonstrate effects of the 4 cover types. The mussel bed at Carrying Place Cove was primarily bare sediment, with substantial cover of whole shells and fragmented shells and almost no live mussels. The combined cover value of whole and fragmented shells was an order of magnitude larger than live mussel cover, revealing the importance of non-living biogenic material when considering the physical structure of this and probably other mussel beds.

4.2. Does biogenic structure matter?

The effects of mussel beds on sediment, ambient community, and ecosystem processes have been well studied in recent years (Bouma et al., 2009; Buschbaum et al., 2009; Commito et al., 2005, 2008, 2014; Gutiérrez et al., 2011; Smith and Shackley, 2004; Thiel and Ullrich, 2002). However, investigations have generally treated mussel beds as a single biotic unit, with little attempt at teasing apart the effects of their different structural components – live mussels, whole shells, and fragmented shells – compared to bare sediment.

We predicted that effects on ambient sediment and organisms, as well as on flow-related sediment flux and animal transport, are greatest for live mussels, followed by fragmented shells and then whole shells. We found significant differences across cover types at the univariate

Cores: Meiofauna

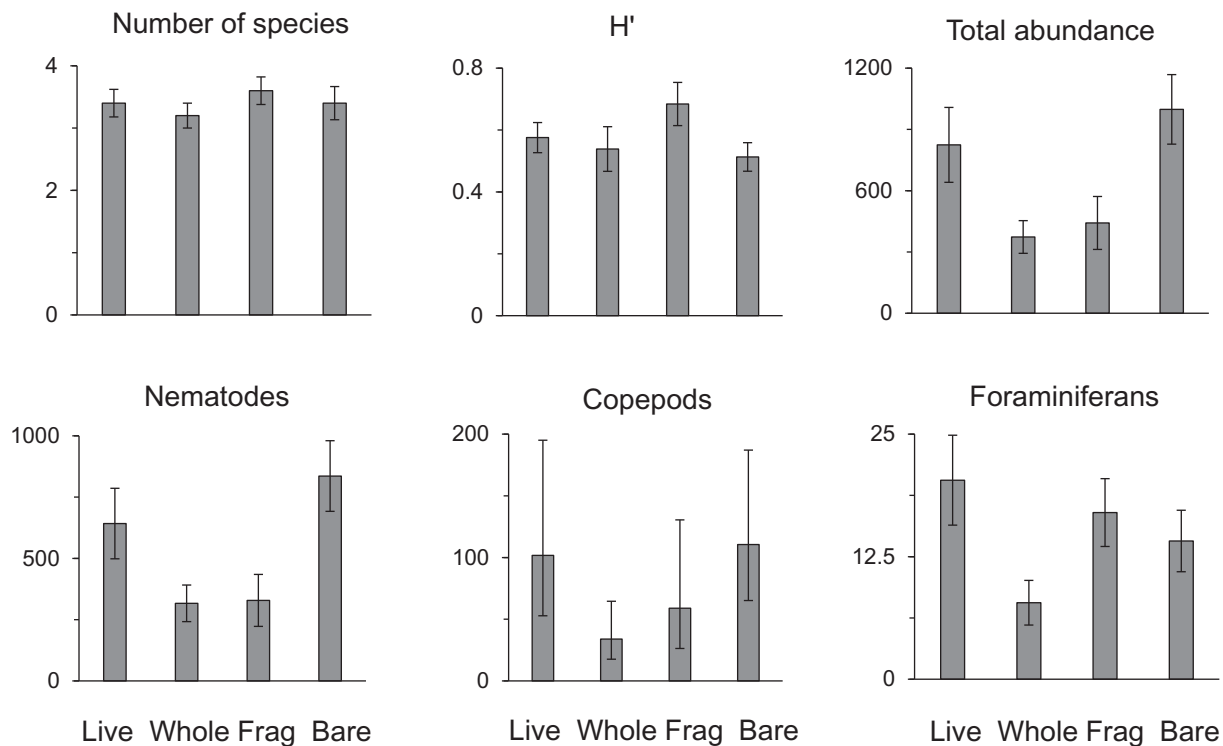


Fig. 7. Meiofauna results for cores. Values are mean \pm 1 SE for number of taxa, Shannon-Wiener diversity index (H'), total abundance, and abundances of the dominant taxa (nematodes, foraminiferans), and back-transformed mean and 95% confidence interval for the dominant taxon of copepods, which required transformation to meet ANOVA assumptions. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. See Results and Table 2 for statistical analysis.

level in sediment structure and animal abundances for both the ambient community and the transported sediment and animals. The fragmented shell cover type was often most different from the others. We also found significant differences at the multivariate level for meiofauna in both ambient community and dispersing assemblage structure. The fragmented shell cover type contributed most to the dissimilarity. Thus it seems that cover type is an important driver in mussel beds and that fragmented shell material may be particularly important.

We studied patches $\geq 0.5 \text{ m} \times 0.5 \text{ m}$ in size for all 4 cover types because we wanted all the patches to be similar in size, and live mussels were never observed in patches larger than this size. Most of our patches were right at the lower size limit. Had we been able to use larger patches with lower perimeter: area ratios, it is possible that the influence of cover type may have been stronger. Thus, our results are likely to be conservative estimates of cover type effects.

4.2.1. Sediment

Organic material in soft-bottom systems is typically linked positively to the silt-clay fraction and negatively to the coarse fraction (Gray and Eliot, 2009). However, despite significant differences in the sediment size-classes among cover types, with bare sediment cover having the most silt-clay and fragmented shell cover having the most coarse material, no significant differences occurred in the percentage of total organic material among cover types in cores or traps. This result was surprising because mussels produce feces and pseudofeces known to enhance local sedimentation and alter sediment structure (Albrecht and Reise, 1994; Albrecht, 1998; Commito et al., 2005; Kent et al., 2017; Ragnarsson and Raffaelli, 1999). However, it is possible that organically rich feces and pseudofeces were exported from patches of live mussels to nearby patches of the other cover types, reducing differences

in organic content (Donadi et al., 2013).

Surface topography is generally roughest for live mussels, less rough for fragmented and then whole shells, and smoothest for bare sediment (Commito and Rusignuolo, 2000). These topographic differences shape hydrodynamic profiles because turbulence increases as a function of the roughness, number, and spacing of patches, as well as the amount of patch edge, with more turbulence at patch edges than at patch centers (Folkard and Gascoigne, 2009; Widdows et al., 2009). The result is generally more sediment erosion and resuspension due to higher turbulent kinetic energy and bed shear stress in patches of physical structure compared to bare sediment (wa Kangeri et al., 2016; Widdows et al., 2009), with increased sediment deposition in *M. edulis* beds (Albrecht and Reise, 1994; Albrecht, 1998; Commito et al., 2008; Ragnarsson and Raffaelli, 1999). Yet in this study we found no significant differences across cover types in total sediment collected by traps. One possible explanation is that the cover type patches were too small to produce an effect. Another possibility is that the differences in physical structure among the cover types, or even the presence of physical structure per se, were not enough to enhance sediment capture dramatically. In fact, the opposite may be true. A surface cover of gravel acts as “bed armor” that reduces bedload transport (Singer and Anderson, 1984). It is possible that live mussels, whole shells, and fragmented shells can also armor the surface, thus countering their effects as sedimentation-enhancing roughness elements.

4.2.2. Macrofauna

Our results revealed little difference in macrofauna among cover types. The only significant ANOVA difference was for the opportunistic polychaete *Capitella capitata*, the numerically dominant species. The ambiguous SNK result allowed the conclusion that its abundance was

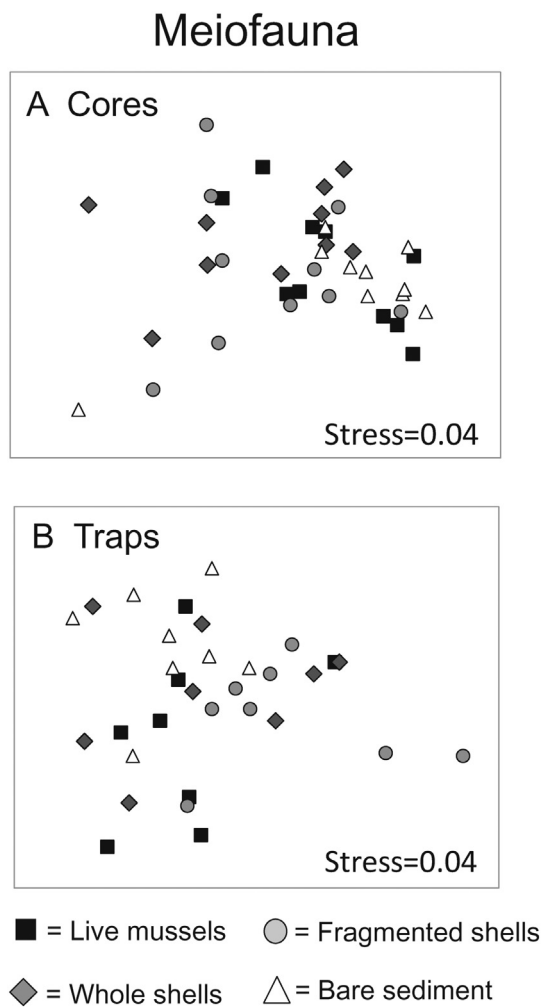


Fig. 8. Non-metric multi-dimensional scaling (nMDS) results for cases where PERMANOVA revealed significant differences among cover types. Meiofauna: (A) Cores, (B) Traps. No significant differences were observed for macrofauna.

higher in live mussel cover than in fragmented shell cover. At the multivariate level, no significant differences were found among cover types. Numerous studies that have found higher total macrofaunal abundance in mussel beds compared to bare intertidal flats, probably due to the production of organically enriched, low oxygen, high sulfide sediment favorable to oligochaetes and opportunistic species like *C. capitata*, especially those without free-swimming larvae (Buschbaum et al., 2009; Commito et al., 2005, 2008; Gutiérrez et al., 2011; Ysebaert et al., 2009). The lack of major differences in macrofauna among cover types in our study most likely reflects the similarities in sediment structure and organic material observed across cover types.

With respect to the dispersing assemblage, macrofaunal abundances in traps are often positively correlated with sediment mass in traps because animals may be transported like passive sediment particles (Commito et al., 1995a, 1995b; 2008; Turner et al., 1997; Valanko et al., 2010a, 2010b). Thus, the lack of clear patterns among cover types for macrofaunal abundance in traps in our study is consistent with the lack of significant differences in total sediment captured by traps.

Our trap results demonstrated that the mussel bed system is highly dynamic, suggesting a potential for change over time. Traps on average collected approximately the same number of macrofaunal individuals in the 3-day deployment as were found in ambient assemblage cores, indicating a turnover time of ≈ 3 days, where turnover time = (no. individuals per core) \div (no. individuals per trap per deployment period). This value is within the range of 1.4–4.3 days at a nearby mussel bed in

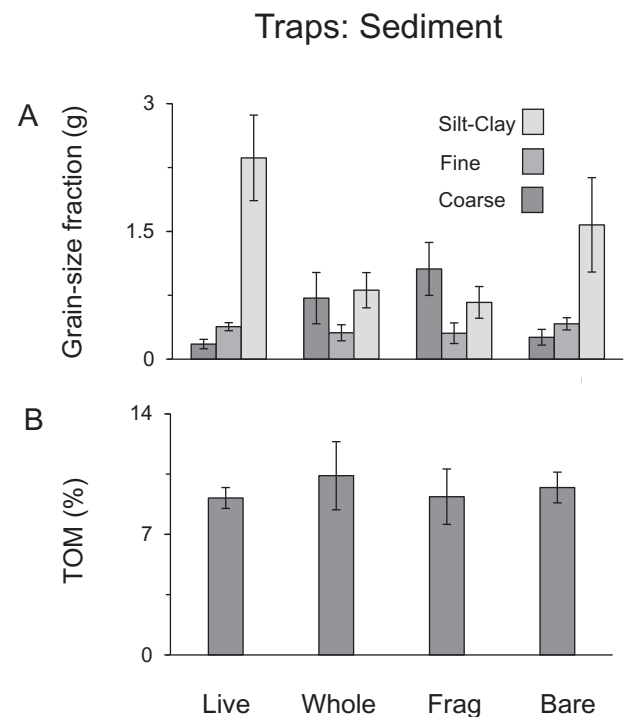


Fig. 9. Sediment results for traps. (A) Mass values of silt-clay (light gray), fine sand (medium gray), and coarse material (dark gray). (B) Percent total organic matter (TOM). Values are mean \pm 1 SE. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. See Results and Table 4 for statistical analysis.

Table 4
ANOVA results for dispersal assemblage traps.

Parameter	Transform	$F_{3,28}$	P	SNK
Sediment				
Total (g)		1.11	0.361	
Silt-clay (g)		5.12	0.006	NAH (Live > Frag)
Fine sand (g)		0.51	0.676	
Coarse material (g)		4.56	0.01	NAH (Frag > Live)
Total organic matter (%)		0.25	0.861	
Macrofauna				
Number of species		0.5	0.688	
H'		0.65	0.591	
Total abundance	Sqrt(X + 1)	0.64	0.595	
Oligochaetes		1.15	0.349	
Non-oligochaetes	Ln(X + 1)	0.16	0.92	
Meiofauna				
Number of taxa		0.64	0.594	
H'	Ln(X + 1)	3.44	0.03	NAH (Bare > Live)
Total abundance	Ln(X + 1)	3.3	0.035	Bare = Whole = Live < F frag
Nematodes	Ln(X + 1)	3.47	0.029	NAH (Bare > Frag)
Copepods		1.86	0.16	
Foraminiferans		3.71	0.023	NAH (Bare > Live)

Significant differences ($P < 0.05$) are in **bold**. For parameters with significant differences among cover types, the SNK results are presented. NAH = no alternative hypothesis; the 2 cover types with the largest and smallest means were significantly different, and no further resolution among cover types was possible. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment.

Maine (Commito et al., 2005) and 2.5–33 days calculated from data in Valanko et al. (2010a, 2010b) for a shallow, non-tidal, subtidal site in the Baltic Sea. It is longer than the range of 0.5–1.1 days for a small bivalve (*Gemma gemma*) at a sandflat in Virginia (Commito et al., 1995a), most likely because the sandflat had high wind velocities, and

Traps: Macrofauna

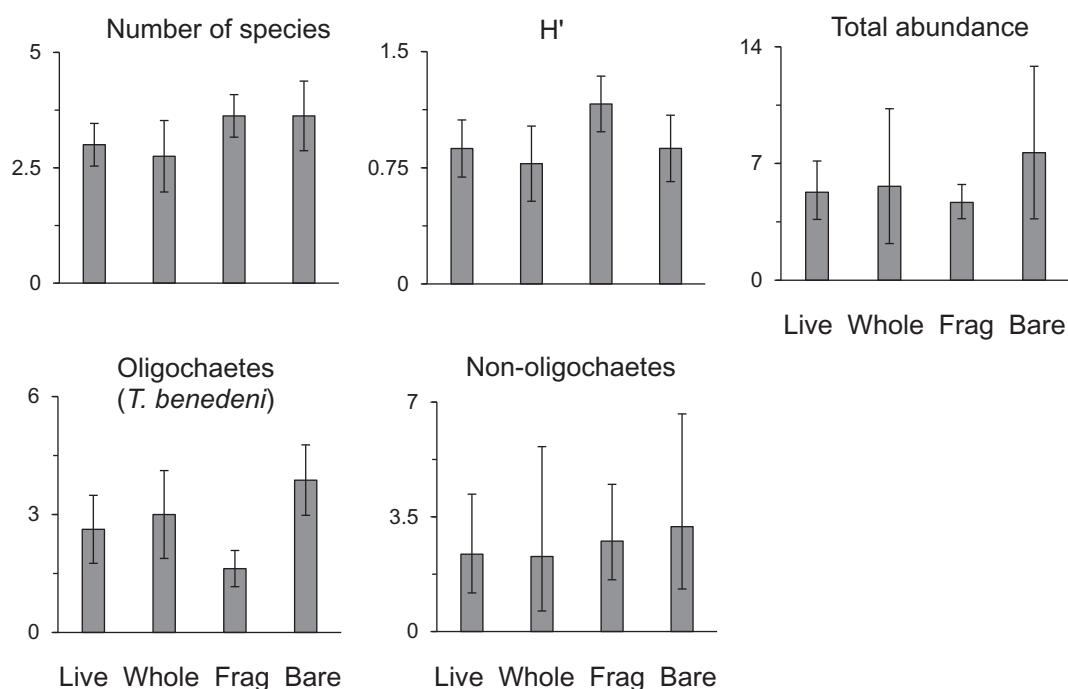


Fig. 10. Macrofauna results for traps. Values are mean \pm 1 SE for number of species, Shannon-Wiener diversity index (H'), and abundance of the dominant species (the oligochaete *Tubificoides benedeni*), and back-transformed mean and 95% confidence interval for total number of individuals and the non-oligochaetes as a group, which required transformation to meet ANOVA assumptions. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. See Results and Table 4 for statistical analysis.

Table 5
PERMANOVA results for dispersal assemblage traps.

Parameter	MS	$F_{3,28}$	P
<i>Macrofauna</i>			
All species	2854.10	0.97	0.522
Without oligochaetes	3466.50	0.86	0.68
<i>Meiofauna</i>	2273.29	2.19	0.043
Within cover type:			
Live = 35.99			
Whole = 49.50			
Frag = 42.71			
Bare = 32.31			
Among cover types:			
Live vs Whole = 41.83			
Live vs Frag = 47.53			
Live vs Bare = 34.07			
Whole vs Frag = 48.02			
Whole vs Bare = 41.05			
Frag vs Bare = 48.12			

Significant differences ($P < 0.05$) are in **bold**. For parameters with significant differences among cover types, the mean Bray-Curtis dissimilarity (%) values within and among cover types are presented. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment.

bedload transport and benthic animal transport are positively related to wind-generated hydrodynamic forces (Committo et al., 1995a, 1995b; Turner et al., 1997; Valanko et al., 2010a, 2010b).

Traps collected macrofauna in different proportions than were found in the ambient community cores. *Tubificoides benedeni*, the dominant macrofaunal species in the ambient community, was the most abundant macrofaunal species in traps but dropped substantially as a proportion of the total. Yet for macrofauna, ambient community structure seems to persist in soft-bottom systems, despite the daily

transport across the bottom of organisms with a different species mix than in cores (Committo et al., 2005; Turner et al., 1997; Valanko et al., 2010a, 2010b). In the face of potential forcing from dispersing organisms, the strength of this resistance to change is a ripe topic for research.

4.2.3. Meiofauna

Cover type had stronger effects on meiofauna than on macrofauna. Significant ANOVA differences were found for total meiofauna and the numerically dominant nematodes. The ambiguous SNK results allowed the conclusion that abundances for both parameters were higher in bare sediment cover than in whole shell cover. At the multivariate level, significant differences in meiofaunal community structure occurred among cover types. Dissimilarity values indicated that fragmented and whole shells had a large impact on the meiofauna community. Some live bivalves (e.g., *Cerastoderma glaucum*, *Macoma balthica*, *Mya arenaria*; Urban-Malinga et al., 2016) are known to enhance nematode, copepod, and total abundance values. We did not find this effect for live *M. edulis*.

With respect to the dispersing assemblage, cover type again had stronger effects on meiofauna than on macrofauna. ANOVA revealed significant differences in several parameters, and total abundance was significantly lower in fragmented shell cover than in the other cover types. One possible explanation is that fragmented shell cover acted as bed armor to reduce the erosion and capture of local, within-patch meiofauna, especially in comparison with bare sediment.

Traps collected 2.3-fold more meiofaunal individuals than were in cores, indicating a turnover time of ≈ 1.3 days, which is shorter than the 4-day turnover time for meiofauna at a nearby Maine mudflat (Committo and Tita, 2002), most likely because wind velocities were higher during this study. As with macrofauna, traps collected meiofaunal taxa in different rank order than were found in the ambient

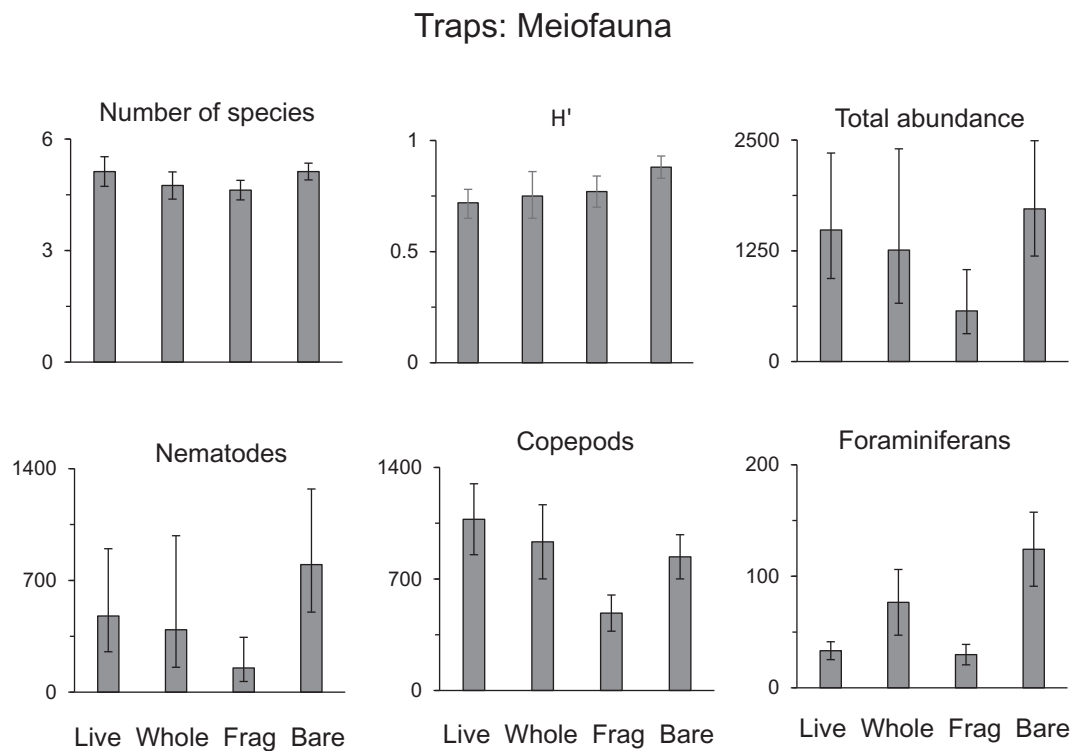


Fig. 11. Meiofauna results for traps. Values are mean \pm 1 SE for number of taxa and abundances of the dominant taxa (copepods, foraminiferans), and back-transformed mean and 95% confidence interval for Shannon-Wiener diversity index (H'), total number of individuals, and the dominant taxon of nematodes, which required transformation to meet ANOVA assumptions. Live = live mussels, Whole = whole shells, Frag = fragmented shells, Bare = bare sediment. See Results and Table 4 for statistical analysis.

community. The rank orders of the 2 dominant taxa in cores, nematodes and copepods, were reversed in traps, with copepods the most abundant taxon by a wide margin, as was also observed in traps at a nearby mudflat (Commito and Tita, 2002). This reversal indicates clearly that copepods and nematodes do not disperse in the same way, most likely because copepods can live close to the sediment-water interface and engage in active emergence from the bottom in response to flow (Commito and Tita, 2002; Pacheco et al., 2013).

4.3. Implications for mussel bed decline

A serious decline in the abundance of intertidal mussels over the past several decades has been documented in the Gulf of Maine, including larvae, juveniles, and adults (Petratis and Dudgeon, 2015; Sorte et al., 2011, 2016). We have observed this decline in eastern Maine, where we have conducted mussel bed research since the mid-1970s. The intertidal, soft-bottom mussel beds in eastern Maine that we have studied over the years typically had \approx 50% cover of live mussels in complex fractal power-law spatial patterns (Crawford et al., 2006). Many formerly robust beds contain virtually no live mussels today (John A. Commito, personal observation; Brian F. Beal, personal communication). They now consist largely of bare sediment with patches of shell hash.

Individual soft-bottom mussel beds can experience short-term population swings (Folmer et al., 2014; Khaitov and Lentsman, 2016; Nehls and Thiel, 1993). But the Gulf of Maine decline encompasses much broader spatial and temporal scales and is generally attributed to climate change (Helmuth et al., 2006; Jones et al., 2010; Lesser, 2016; Sorte et al., 2011, 2016) and predation by the invasive green crab, *Carcinus maenas* (Grosholz and Ruiz, 1996; Tan and Beal, 2015; Whitlow and Grabowski, 2012). The decline may also be related to long-term oscillating oceanographic conditions in the northwest Atlantic region (Beaugrand et al., 2008; Edwards et al., 2013; Greene

et al., 2013). Thus it may be premature to state with certainty that a permanent Gulf of Maine regime shift is occurring. Regardless of the reasons behind the reduction in mussels, their decline means that bottom cover values of whole shells, fragmented shells, and bare sediment are likely to be increasing relative to live mussels. To the degree that Carrying Place Cove may serve as a general model for a mussel bed that has suffered declines, our results can be useful in helping to predict the responses to these changes.

As mussels die from causes that do not affect the shell directly, they produce an increase in whole shell cover, followed by breakdown into coarse fragmented shell pieces. Crushing and chipping predators like *Carcinus maenas* contribute directly to the production of coarse shell fragments (Tan and Beal, 2015). In addition, whole and fragmented shells held by mussel byssal threads (Commito et al., 2014) are released as mussels die. Moreover, in our study we found that coarse material was captured at higher rates in fragmented shell cover than in bare sediment, a form of positive feedback that may contribute to the maintenance of the fragmented shell cover type. Despite this increase in shell hash, our transect results showed that bare sediment by far comprised the largest bottom cover area in the Carrying Place Cove mussel bed. This result suggests that shell material is probably being exported, buried, or broken down into fine particles. Interestingly, although we have observed changing relative values of each cover type at Carrying Place Cove over the past several decades, the boundaries of the mussel bed have remained stationary. Live mussels are still present at the upper (landward) and lower (seaward) margins of the bed. We observe some internal shifting of whole and fragmented material on a daily basis, apparently resulting in net transport to the upper part of the bed, as seen in Fig. 4. We can find windrows of whole and fragmented mussel shells along the shoreline above the mussel bed. But unlike storm-induced movement of empty snail shells described by Nicastro et al. (2009), relatively little mussel shell material at our site seems so far to have been exported outside of the original bed boundary, perhaps due

to its position in a sheltered embayment.

Small patch size may be at least partly responsible for the relatively small differences we found across cover types for many parameters. Small patch size may be the norm as intact mussel beds die off and large patches of live mussels give way to small patches of live mussels, whole shells, and fragmented shells scattered within large areas of bare sediment. Intact mussel beds and other bivalve reefs are important ecosystem engineers and provide valuable ecosystem services (Borsje et al., 2011; Bouma et al., 2009; Buschbaum et al., 2009; Commito et al., 2005, 2008; Gutiérrez et al., 2011; Koch et al., 2009; Palumbi et al., 2009; Stone et al., 2005). If patches reach a small enough size, then a tipping point may be reached when the system is no longer a functional mussel bed. Then its ecosystem engineering effects will be gone, as will the ecosystem services it once provided.

5. Conclusion

M. edulis beds comprise a spatial mosaic of live mussels, whole shells, fragmented shells, and bare sediment. Sediment and benthic fauna differ among these cover types, as do their rates of movement in bedload. Particularly in regions such as the Gulf of Maine, where mussel beds may be declining in response to factors including climate change and invasive predators, consideration of these differences will lead to better understanding of the ecology of mussel beds and soft-bottom systems overall.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2018.05.004>.

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